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A NEW BASIDIOBOLUS THAT FORMS MICROSPORES

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When Eidam, in 1886, established *Basidiobolus* as a new genus of saprobic Entomophthoraceae he described the type species, *B. ranarum,* from the intestinal contents of two species of frogs, *Rana esculenta* and *R. oxyrhina,* and *B. lacertae* from the dung of a lizard, *Lacerta agilis.* Several years later, Fries (1899) described *B. myxophilus* from zoogloea associated with a rotting coniferous stump, and in a recent series of definitive papers on *Basidiobolus,* Drechsler (1947, 1955a, 1956a, 1958) summarized previous taxonomic work on the genus and described two additional species, *B. haptosporus* (Drechsler, 1947, 1956a) and *B. meristosporus* (Drechsler, 1955a).

The status of *Basidiobolus lacertae* and *B. myxophilus* as species distinct from *B. ranarum* is subject to question. Indeed, after reconsidering his evidence, Fries (1929) relegated *B. myxophilus* to synonymy with *B. ranarum.* Eidam first encountered *Basidiobolus* in the intestinal contents of a lizard, *Lacerta agilis* (Eidam, 1886, p. 239), but he never succeeded in culturing this fungus, and described *B. lacertae* after restudy of admittedly scanty preserved material. This work led him, however, to his discovery and detailed description, based in part on pure cultures, of *B. ranarum* from frogs. *Basidiobolus lacertae* was said to differ from *B. ranarum* because of (1) a poorly developed mycelium, often with thick-walled terminal cells, (2) the more slender and more sharply pointed apex of the "basidium"—that portion of the subsporangial swelling which separates and is carried away with the discharged spore (see fig. 1m), and (3) the shape of the zygospore and absence of cross walls delimiting terminal cells in the paired protuberances of the gametangia characteristic of this genus (fig. 2 h–j). In 1903, Loewenthal, without benefit of pure cultures, presented an account of a *Basidiobolus* derived from globose cells—which he termed "Darmform"—found in the intestinal contents of another lizard, *Lacerta muralis.* Although Loewenthal assigned the name *B. lacertae* to his fungus, it is evident that this was done primarily because of its occurrence in a lizard. He observed (Loewenthal, 1903, pp. 397–398), in his material, a mingling of the characteristics listed by Ediam for *B. ranarum* and *B. lacertae,* and, although recognizing the possibility that two species might have been present in his lizards, he dismissed the problem of the true identity of his fungus as follows, "Ich glaube im folgenden *B. lacertae* und *B. ranarum* ohne weiteres mit einander vergleichen zu durfen." In another definitive work on the development of *Basidiobolus* from "Darmform" found in the intestines of frogs, Levisohn (1927) considered the question of *B. lacertae* versus *B. ranarum* at some length and concluded that they are idenitcal. Pending further evidence to the contrary, *B. lacertae* and *B. myxophilus* probably should be considered synonymous with *B. ranarum.*

Although *Basidiobolus ranarum* commonly has been encountered as a saprobe in excreta of frogs and lizards, the species also has been found in intestinal contents of salamanders (Levisohn, 1927) and appears to be common in humus (Möller, 1901; Drechsler, 1955a, 1956a). *Basidiobolus meristosporus* too has been isolated from frog dung but, along with

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B. haptosporus, also has been frequently encountered in soil (Drechsler, 1955a, 1956a).

A species of *Basidiobolus* tentatively identified as *B. ranarum* was isolated recently from subcutaneous lesions in several human patients in Indonesia (Emmons, et al., 1957); the identity of this fungus, studied in detail by Drechsler (1958), still is open to question, for it displays several characteristics, including smooth zygospores, not common to *B. ranarum.* When additional isolates of this fungus are available, it may prove to be a distinct species.

In 1927, Léger presented evidence that *Ichthyophonus intestinalis* Léger and Hesse (1923), parasitic in trout and salmon, actually is a *Basidiobolus,* for cultures of "spherules" taken from infected fish and presumed to be a stage in the life cycle of *I. intestinalis* gave rise to mycelia bearing asexual and sexual structures characteristic of *Basidiobolus.* Léger then suggested that the well-known fish parasite, *Ichthyosporidium hoferi* (Plehn and Mulsow) Pettit (1911; syn. *Ichthyophonus hoferi*), also is a *Basidiobolus.* Léger's conclusion apparently has not been considered seriously by more recent students of *I. hoferi* who have retained the genus *Ichthyosporidium* (Fish, 1934; Sproston, 1944; Sindermann and Scattergood, 1954; see also the review by Johnson and Sparrow, 1961), and parasitism of fish by *Basidiobolus* needs confirmation. Léger (1927) did not effect formal transfer of *Ichthyophonus intestinalis* to *Basidiobolus;* the name *B. intestinalis,* cited by Drechsler (1955a), was not validly published.

At present, then, three well-defined species of *Basidiobolus* may be recognized, *B. ranarum, B. haptosporus,* and *B. meristosporus.* In his recent papers, Drechsler (1947, 1955a, 1956a, 1958) has discussed and illustrated these species in great detail and only a brief summary of their characteristics need be presented here.

All three species grow readily in pure culture on various media such as nonsupplemented corn meal agar and produce branched vegetative mycelia that become divided by cross walls into usually relatively short uninucleate hyphal segments. The substrate mycelium of *B. haptosporus,* according to Drechsler (1956a), often is relatively inconspicuous in contrast to that of *B. ranarum* and *B. meristosporus,* and the last species characteristically gives rise to well-defined aerial mycelia. Drechsler also observed that *B. ranarum* gives off a strong *Streptomyces*-like odor resembling benzene hexachloride whereas *B. haptosporus* and *B. meristosporus* do not. Drechsler (1956a) has shown that zygospores of all three species at first are uninucleate but become binucleate at maturity and give rise on germination to binucleate germ hyphae or sporophores bearing binucleate spores. On resumption of the vegetative state, however, the uninucleate condition is restored.

Even in young cultures of *B. ranarum* and *B. meristosporus* asexual and sexual reproduction usually proceed concurrently. In *B. haptosporus,* however, an active mycelium often is nearly void of asexual reproductive structures whereas zygospores may be produced in abundance. The germinating zygospores of this species are often more productive of sporophores than the hyphal segments (Drechsler, 1956a). The outer wall of the mature zygospore of *B. ranarum* is undulate as seen in optical section whereas it is smooth in *B. haptosporus* and *B. meristosporus.*

In all known species of *Basidiobolus,* globose spores are discharged violently by rupture of the expanded distal portions of sporophores (fig. 1 g–m) arising from hyphal segments or, secondarily, from other globose spores. In addition, a second type of spore, probably observed by Eidam (1886, Pl. 9, fig. 16) but misinterpreted, has been demonstrated by Drechsler in all of the species of *Basidiobolus* he has studied. This secondary-type spore (Drechsler, 1947), formed terminally on a long slender stalk arising from a primary-type globose spore or from another secondary-type spore, is strobiliform in shape with a usually short slender beak terminating in a globular mass of adhesive material (fig. 1 a–b). These elongate adhesive spores are not discharged violently but become detached by the slightest

disturbance and have been observed in great numbers attached to mites infesting old cultures (Drechsler, 1956a). The utility of such spores in effecting dissemination by small animals can hardly be questioned and recalls a similar dispersal mechanism found in several predacious fungi including *Dactylella asthenopaga* Drechsler (1937), *Stylopage rhynchospora* Drechsler (1939), *Dactylaria haptospora* Drechsler (1940b), *Nematoctonus leptosporus* Drechsler and *N. pachysporus* Drechsler (1943), *Gonimochaete horridula* Drechsler (1946), and *Meristacrum asterospermum* Drechsler (1940a). The secondary-type spores of *Basidiobolus,* like the primary-type globose spores, are capable of immediate germination on a suitable medium. Secondary elongate spores, which, however, lack adhesive beaks, also have been described in five species of *Conidiobolus: C. heterosporus* Drechsler (1953), *C. rhysosporus* Drechsler (1954), *C. rugosus* Dreschler (1955c), *C. pumilus* Drechsler (1955b), and *C. globuliferus* Drechsler (1956b). Similar spores, also without adhesive beaks, were described and figured by Thaxter (1888) for *Empusa fresenii* Nowakowski, *E. lageniformis* Thaxter, *E. lampyridarum* Thaxter, *E. geometralis* Thaxter, *E. occidentalis* Thaxter, and *E. sphaerosperma* (Fres.) Thaxter.

In *Basidiobolus,* both globose- and elongate-type spores may function as sporangia by forming internal sporangiospores through three-dimensional segmentation of their contents (Drechsler, 1947, 1955a, 1956a, 1958). It should be noted, however, that sporangiospore formation in the *Basidiobolus* sporangium is progressive (fig. 3 a–d) rather than simultaneous as in the typical multisporous sporangium of the Mucorales. Endogenous sporangiospores have not yet been demonstrated in other members of the Entomophthorales. However, in *Delacroixia coronata* (Costantin) Saccardo and Sydow (1899) and four species of *Conidiobolus, C. brefeldianus* Couch (1939), *C. chlamydosporus* Drechsler (1955d), *C. polytocus* Drechsler (1955d), and *C. megalotocus* Drechsler (1955b), globose primary-type spores often give rise to several short projections bearing single smallish spores termed microconidia by Drechsler who has alluded to their possible homology with the sporangiospores of *Basidiobolus* and members of the Mucorales (Drechsler, 1955d). This idea is strengthened by the discovery of the following species of *Basidiobolus* in which primary-type globose spores typically give rise to large numbers of a distinctive-type microspore borne singly on slender protuberances (fig. 2 c, 3 e).

Basidiobolus microsporus sp. nov.

Coloniae in agaro YpSs incoloratae; hyphis vegetantibus ramosis, plerumque 8–20 μ diam., mox septatis; cellulis plerumque 30–200 μ longis, uninucleatis; sporophoris primariis singillatim ex cellulis mycelii vel ex sporis globosis surgentibus, incoloratis, nonramosis, 7–16 μ latis, 200–500 μ longis, sursum in tumoribus jaculatoriis 50–80 μ longis et 20–36 μ latis inflatis, apice sporam primariam singularem ferentibus, deinque hunc violenter abjicientibus; sporis primariis globosis, 28–41 μ diam., basi unam papillam praeditis, incoloratis, nucleum solum continentibus, saepe intus 8–60 (med. 35) cellula gignantibus; cellulis contentis extus pediculos 5–10(–20) μ longos, basi 1.5–2.2 μ latos, apice 1–1.3 μ latos, gerentibus; pediculis microsporam singulam terminalem gerentibus; microsporis incoloratis, 15–40 μ longis, in cellula uninucleata ovoidea, 7–11 μ longa $\times$ 4.4–6.6 μ lata, et apice elongato attenuato, 7–28 μ longo, basi 1.3–2.2 μ lato, consistentibus; zygosporis ex conjugio 2 cellularum contiguarum in hyphis mycelii vel in sporis primariis formatis, globosis, 20–44 μ (med. 33 μ) diam. vel ovoideis, 20–42 μ latis $\times$ 22–52 μ longis; muro flavido, undulato, 2–7 μ (med. 5 μ) crasso.

Colonies on YpSs agar colorless, readily visible; vegetative hyphae branched, mostly 8–20 μ in diam., early becoming divided by cross walls; hyphal segments mostly 30–200 μ long, uninucleate; primary sporophores arising singly from hyphal segments or from globose spores, colorless, unbranched, 7–16 μ wide, 200–500 μ long, inflated distally into

propulsive swellings 50–80 μ long and 20–36 μ wide, each bearing at its tip a single primary spore and forcibly shooting it off; primary spores globose, 28–41 μ in diam., each with a wide basal mammiform protrusion, colorless, uninucleate, often forming 8–60 (aver. 35) cells internally, each of which gives rise externally to a single slender pedicel 5–10 (–20) μ long, 1.5–2.2 μ wide below, 1–1.3 μ wide above, bearing a microspore terminally; microspores colorless, 15–40 μ long, each composed of a uninucleate, ovoid basal cell 7–11 μ long × 4.4–6.6 μ wide, and an attenuated apical projection 7–28 μ long, 1.3–2.2 μ wide at the base; zygospores originating from the union or two contiguous cells either in mycelial hyphae or in primary spores, globose, 20–44 μ (aver. 33 μ) in diam., or ovoid, 20–42 μ wide × 22–52 μ long; wall yellowish, undulate, 2–7 μ (aver. 5 μ) thick.

Holotype.—**CALIFORNIA.** Inyo County: 1 mile east of Tecopa Pass, April 22, 1960, isolated from dung of small animal (RSA Culture 977).

Other specimens.—**CALIFORNIA.** San Diego County: 5 miles northwest of Agua Caliente Hot Springs, April 5, 1960, isolated from dung of small animal (RSA Culture 962). San Bernardino County: 10 miles west of Barstow, May 23, 1960, isolated from duff beneath nest of pack rat (RSA Culture 982). Transfers of the holotype have been deposited in the culture collections of the American Type Culture Collection, Washington, D.C., Centraalbureau voor Schimmelcultures, Baarn, Netherlands, and Commonwealth Mycological Institute, Kew, England.

In plate cultures on YpSs agar[2], subsurface vegetative mycelia of *B. microsporus* are composed mostly of branched, relatively long and narrow hyphae (fig. 1 c) often having terminal cells 600–700 μ long by 8–20 μ wide prior to formation of cross walls. Intercalary cells are extremely variable in length and range from about 30–200 μ long. As the colony expands, most of the older intercalary cells are devoid of cytoplasm as this is expended in the formation of sexual reproductive structures or advancing hyphal branches. Near the surface—the region of active sporophore formation—hyphal segments usually are shorter and somewhat wider than those below and are mostly 15–40 μ in diameter. Hyphal segments are uninucleate. In aged cultures, chlamydospore-like bodies (fig. 1 f) often may be produced in limited numbers.

The culture medium greatly influences vegetative characteristics of *B. microsporus*. Growth and development on NsCM resembles very closely that on YpSs but is less vigorous; segments of advancing hyphae tend to be relatively long compared to their diameter, and globose to subglobose chlamydospore-like hyphal bodies are only occasionally formed.

[2]Constitutions of media per liter of distilled water are as follows: YpSs *(Yeast extract soluble starch agar)*.–Yeast extract, 4 g; soluble starch, 15 g; K_2HPO_4, 1 g; $MgSO_4 \cdot 7H_2O$, 0.5 g; agar 20 g.—ME-YE *(Malt extract yeast extract agar)*.–Malt extract, 3 g; yeast extract, 3 g; peptone, 5 g; dextrose, 10 g; agar, 20 g.—SMA *(Synthetic mucor agar)*.–Dextrose, 10 g; asparagine, 2 g; KH_2PO_4, 0.5 g; $MgSO_4 \cdot 7H_2O$, 0.5 g; thiamine chloride, 0.5 mg; agar, 15 g.—NsCM *(Nonsupplemented corn meal agar)*.–Corn meal, 25 g, cooked for 10 min. in 700 cc of water and strained through a porous cloth; agar, 20 g; enough water to bring the volume to 1 liter.

Fig. 1. a. *Basidiobolus ranarum* Eidam.—Elongate adhesive spore borne terminally on a slender stalk that has arisen from a globose spore. × 230.—b. *Basidiobolus meristosporus* Drechsler.—Elongate adhesive spores; one is still attached to its slender stalk that arose from a globose spore. × 230.—c–m. *Basidiobolus microsporus* Benjamin.—c. Typical assimilative hypha of fungus growing on YpSs agar; note single nucleus in the terminal cell and young lateral branch. × 340.—d. "Darmform"-like hyphal bodies formed by vegetative hypha deep within agar of plate culture on ME-YE. × 340.—e. Proliferating hyphal bodies characteristic of surface growth of fungus on SMA. × 340.—f. Chlamydospore-like cells accompanying zygospores in aged culture on YpSs. × 340.—g–k. Several stages of development of globose spores from terminal enlargements of sporophores. × 340.—m. Collapsed terminal enlargement of sporophore with globose spore still attached; note conformation of that portion of the swelling—the "basidium"—which typically is carried away with the spore when it is discharged. × 340. (a–b. Specimens mounted in KOH-phloxine; c–m. Living material mounted in water.)

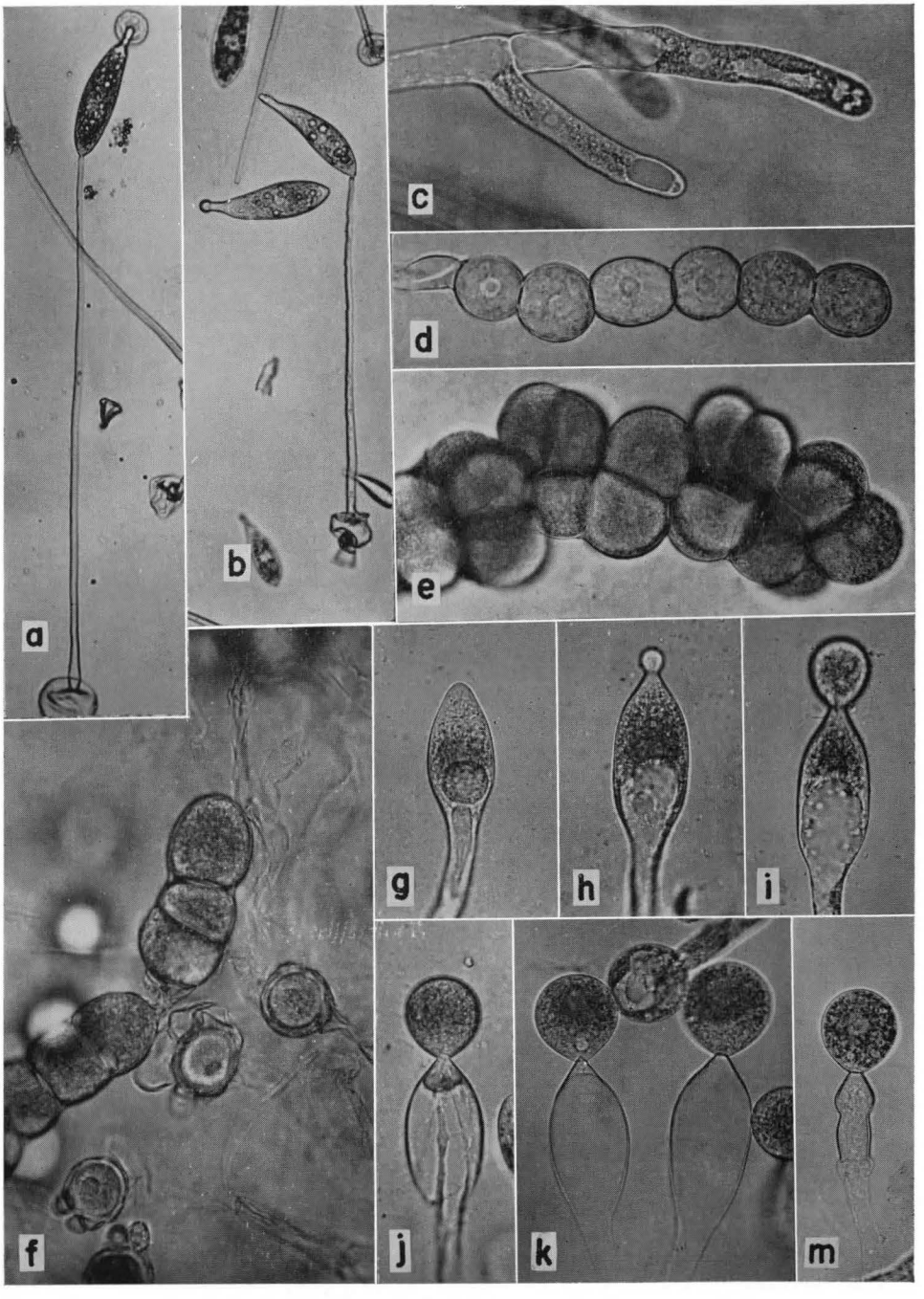

FIGURE 1

After about 4 days at room temperature (22–25°C), colonies on YpSs may reach diameters of 15–20 mm, but on NsCM they may have diameters of only 5–7 mm. Except for sporophores, colonies on these media do not extend noticeably above the surrounding agar surface. On relatively rich media such as ME-YE and SMA, vegetative hyphae tend to form elongate hyphal cells only some distance below the surface of the substratum and these often are soon converted into globose or subglobose hyphal bodies (fig. 1 d) very reminiscent of the "Darmform" described by Levisohn (1927) and Loewenthal (1903) for *B. ranarum* in the intestines of frogs and lizards. I also found similar cells in abundance in cultures of *B. ranarum* and *B. meristosporus* growing on ME-YE and SMA. After about 4 days at room temperature, colonies of *B. microsporus* on ME-YE reach diameters of 8–13 mm whereas on SMA these usually are only 1.5–4 mm in diameter. At or near the surface of the substratum, colonies on ME-YE and SMA are composed almostly exclusively of globose or subglobose hyphal bodies (fig. 1 e) that often form rugose mounds extending a millimeter or more above the surrounding surface.

On none of the media employed here have any of my isolates of *B. microsporus* given off the distinctive odor of benzene hexachloride described by Drechsler for *B. ranarum*. An isolate of the latter species from Claremont, California (RSA Culture 334), consistently produces such an odor in culture; an isolate of *B. meristosporus*, also from Claremont (RSA Culture 964) does not.

Production of primary-type sporophores from hyphal segments or discharged globose spores does not differ in *B. microsporus* in any essential detail from that observed in *B. ranarum, B. haptosporus,* and *B. meristosporus*. This process was very adequately described by Drechsler (1955a, 1956a). Figure 1 g–m illustrates formation of primary-type globose spores from the expanded distal portions of sporophores.

As in other known species of *Basidiobolus*, sexual and asexual reproduction proceed concurrently in *B. microsporus* and may begin in colonies only 2–3 days old, especially on YpSs and NsCM. On ME-YE and SMA zygospore formation may be delayed a week or more. Conjugation typically takes place between adjacent hyphal segments (fig. 2 h–i) and involves the formation of paired juxtaposed protuberances in the tips of which single nuclei are isolated following division of the gametangial nuclei. Although these terminal cells usually are devoid of cytoplasm following union of gametes and maturation of zygospores (fig. 2 j), they may remain alive (fig. 2 n). I never have observed development of hyphae from these cells. Mature zygospores have thick walls consisting of two distinct layers often partially separated (fig. 2 k–m). The inner wall is smooth, the outer distinctly undulate. Not uncommonly, primary-type spores form zygospores in the typical manner following formation of longitudinal septa (fig. 2 o–q). A similar phenomenon was reported in *B. meristosporus* by Drechsler (1955a, p. 56) for both globose and adhesive spores.

Secondary adhesive-type spores like those of *B. ranarum* (fig. 1 a), *B. meristosporus*

Fig. 2. *Basidiobolus microsporus* Benjamin.—a. Early stage of development of sporangiospores inside globose spore. × 570.—b. Early stage of development of exogenous microspores from sporangiospores formed inside globose spore. × 570.—c. Mature microspores still attached to pedicels on body of globose spore. × 570.—d. Germinating microspores. × 310.—e. Two microspores showing variation in length of apical prolongations. × 1300.—f–g. Two microspores stained to show single nuclei in living cells. Fig. f shows point of dehiscence of spore from pedicel. × 1300.—h. Early stage of sexual reproduction showing conjugation of adjacent hyphal segments. × 310.—i. Sexual structures showing paired protuberances and young zygospore. × 310.—j–m. Three mature zygospores. Note empty terminal cells of paired protuberances in j, and partial separation of the inner and outer walls of the zygospores shown in k and m. × 620.—n. Sexual structures showing terminal cells of paired protuberances that are still living. × 620.—o–q. Three stages of development of zygospores from cells formed by longitudinal division of globose spores. × 465. (a–c. Specimens mounted in KOH-phloxine; f–g. Specimens in propiono-carmine; all others from living material mounted in water.)

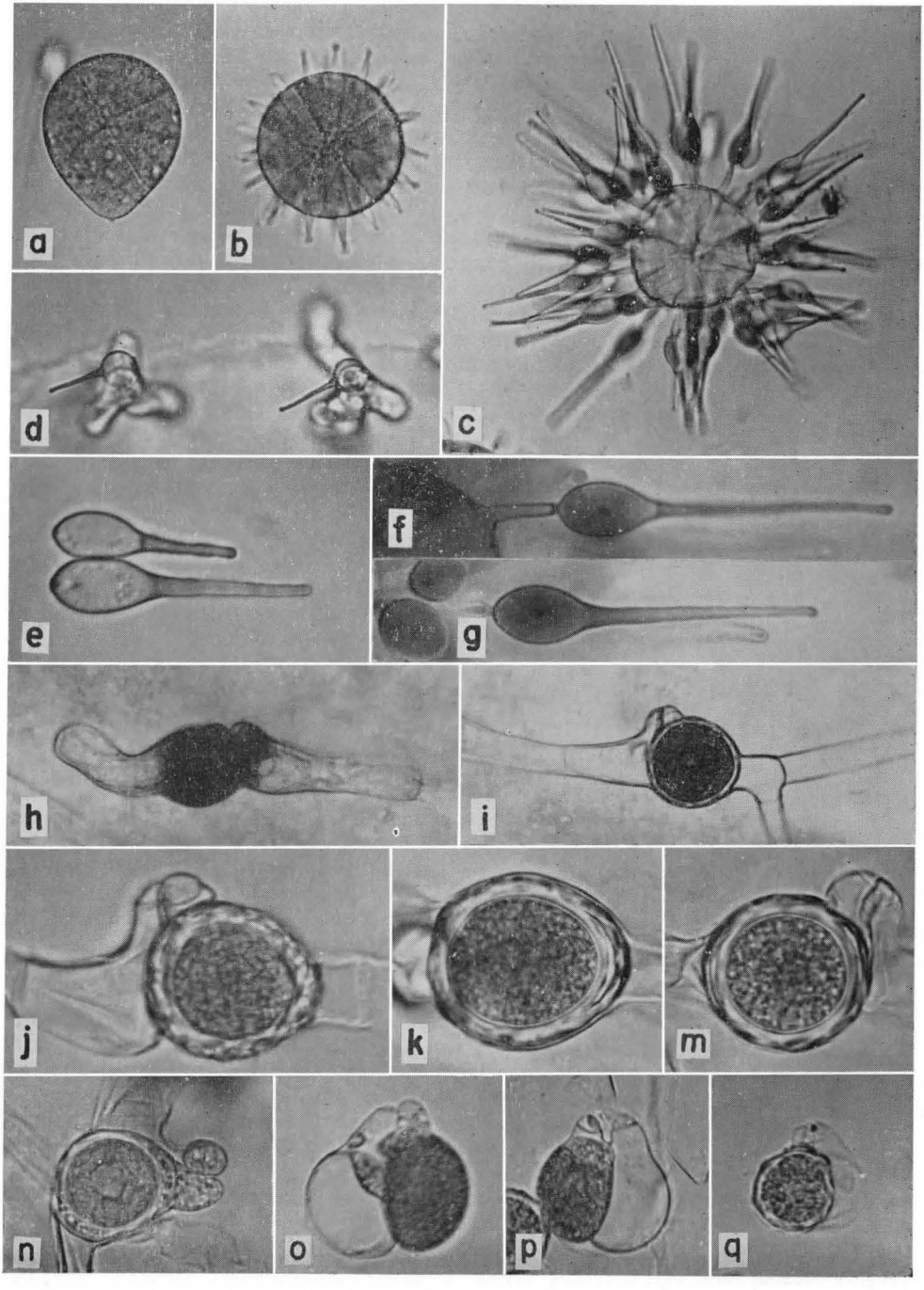

FIGURE 2

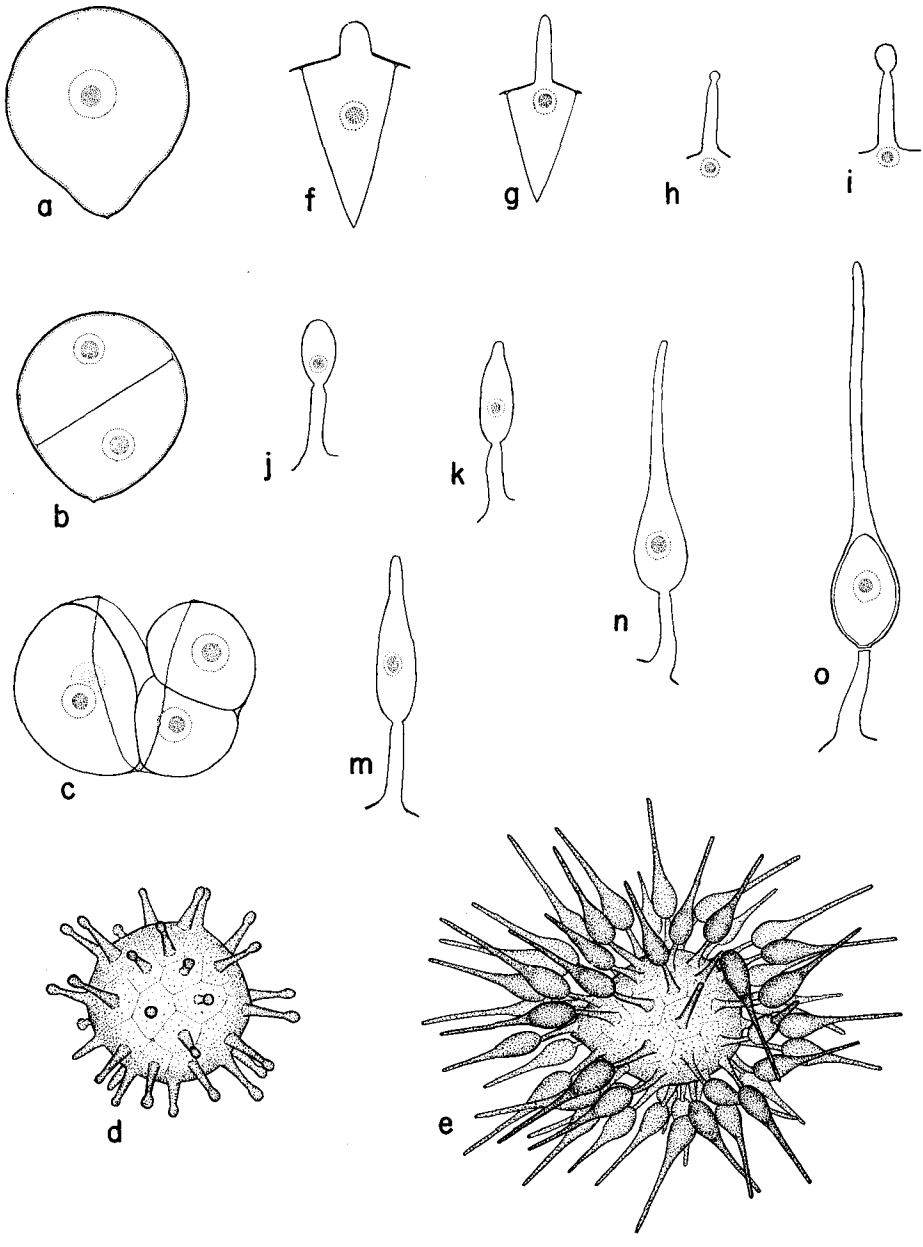

Fig. 3. *Basidiobolus microsporus* Benjamin.—a. Globose spore just after discharge from sporophore showing single nucleus. × 660.—b. First stage in the formation of sporangiospores inside a globose spore. × 660.—c. Four-cell stage in the development of a sporangium from a globose spore; the sporangial wall has been ruptured in order to show separation of internal cells. × 660.—d. Mature sporangium showing initial stage of development of microspores terminally on pedicels arising singly from

(fig. 1 b), and *B. haptosporus* never have been observed in *B. microsporus*.

The one characteristic that readily distinguishes *B. microsporus* from the other known species of *Basidiobolus* is the formation of often relatively large numbers of a unique exogenous spore—here termed a microspore—by discharged primary-type spores (fig. 2 c, 3 e). When primary-type spores fall on an exposed agar surface they may (1) germinate and form new colonies, (2) give rise to sporophores bearing primary-type spores, (3) divide longitudinally and form zygospores following conjugation of adjacent cells, or (4) by internal division form numerous cells (sporangiospores) each giving rise to a single microspore borne externally on a slender protuberance. Zygospore formation from these spores appears to take place most commonly in aged cultures. Direct germination and repetitive formation of sporophores are relatively common on fresh agar, especially in the presence of free water, although microspores also are often formed under such conditions. Under relatively dry circumstances microspores may be formed almost exclusively, as when spores are deposited upon the glass walls above cultures in Petri dishes and culture tubes. In one test, of 347 spores deposited upon a microscope slide placed under an inverted colony 303, or 87%, were forming microspores after 16 hours. Other experiments gave similar results. Mature microspores germinate readily (in less than 24 hours) when implanted on a suitable medium (fig. 2 d).

Sporangiospore formation begins with division of the single nucleus in a discharged globose spore (fig. 3 a); this is followed by cleavage of the spore contents (fig. 2 b). Subsequent divisions (fig. 2 a, 3 c) result in the formation of often large numbers of uninucleate spore-like bodies within the original spore (fig. 2 b, 3 d). These cells undoubtedly are homologous with the sporangiospores formed in primary-type spores of *B. meristosporus* (Drechsler, 1955a) and can be separated from one another if the sporangial wall is ruptured (fig. 3 c). Each sporangiospore may give rise to a single microspore, but not uncommonly several spores in a sporangium in contact with nutrient agar may germinate and form mycelia while the remaining spores form microspores.

Microspore development first is evidenced by the appearance of a papillate outgrowth from each sporangiospore (fig. 3 f). These papillae elongate rapidly and form the microspore pedicels (fig. 3 g–h). The microspore itself then develops from the apex of the pedicel as shown in fig. 3 h–o. The entire contents of the sporangiospore moves into the developing microspore, and the nucleus usually enters when the young spore has reached the stage of development shown in fig. 3 j. When the spore is mature, its nucleus and cytoplasm occupy only the expanded basal portion (fig. 2 f–g, 3 o), and the spore prolongation is empty. Microspores separate passively from their pedicels following formation of septa at the juncture of spore and pedicel (fig. 2 f, 3 o). Adhesive material like that enveloping the beaks of the secondary elongate spores in other known species of *Basidiobolus* (fig. 1 a–b) is absent.

The microspore pedicel apparently is composed of an extension of the wall of the globose spore and the delicate membrane surrounding the endogenous sporangiospore. Utilizing methods of optical microscopy available to me (bright-field and phase-contrast), I have not been able to distinguish the two layers, but the continuity of the sporangial wall and the pedicel wall is readily observed. The microspore, notwithstanding its origin from a sporangiospore, is conidium-like in that distinct spore and sporangial walls are not apparent.

In *B. microsporus* the small microspores, readily detached from their pedicels, doubt-

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each sporangiospore. × 660.—e. Sporangium showing mature microspores still attached to their pedicels. × 660.—f–o. Several stages of development of microspores from sporangiospores. Note position of nuclei during the various stages. (All drawings prepared using material mounted in propionocarmine; no attempt has been made to depict cell contents other than nuclei.)

lessly aid dispersal. Furthermore, it is suggested that they may aid survival under arid conditions. The three strains of the fungus obtained have been isolated from materials collected in the deserts of southern California. Discharged primary-type spores which adhere to relatively dry objects in the vicinity of a developing mycelium nearly all form microspores quickly and in large numbers. Data are not available regarding longevity of microspores, but they germinate readily under proper conditions. Direct germination and repetitive sporophore formation by primary-type spores take place most readily in the presence of free water and would be of benefit to the fungus under relatively moist conditions. Such conditions may, of course, obtain for a short period of time following rain in the desert, but rapid dessication is the rule following the return of fair weather. An asexual spore like the microspore of this species, formed quickly and in large numbers, very well may represent an adaptation to arid conditions.

The species of *Basidiobolus* recognized by the author may be separated as follows:

A. Outer wall of the zygospore undulate ..... *B.*
AA. Outer wall of the zygospore smooth ..... *C.*
B. Microspores absent; colonies with a strong *Streptomyces*-like odor ..... *B. ranarum*
BB. Exogenous microspores formed by globose primary spores; no *Streptomyces*-like odor ..... *B. microsporus*
C. Vegetative mycelium inconspicuous; no aerial hyphae; meager production of sporophores from hyphal segments ..... *B. haptosporus*
CC. Vegetative mycelium conspicuous; many aerial hyphae; abundant production of sporophores from hyphal segments ..... *B. meristosporus*

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